

THE SURFACE FEATURES OF THE BRAIN OF THE HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*)

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INTRODUCTION

Being highly adapted to an aquatic mode of life, the Cetacea present an interesting study both from a morphological and a functional point of view. This applies especially to the brain in these animals as owing to the particular environment in which they have undergone their development, some of the factors responsible for the form and proportions of the brain in living members of the group must have been very different from those operating in the majority of terrestrial mammals.

There are many gaps in our knowledge of the cetacean brain largely because of the difficulty of obtaining specimens in a suitable state for histological examination. As far as can be determined, the literature dealing with the brain of the humpback whale consists of two illustrations of Eschricht's (1869) and a brief account of a foetal brain by Guldberg (1885), together with one or two papers by Riese (1928, 1936) dealing with certain aspects of its development.

Accordingly, as some time ago the brain of an adult humpback whale in a reasonable state of preservation became available it was felt that a brief description might be of value. The present account is confined to the gross features and is largely given from the point of view of comparison with previous accounts of other cetacean brains. It is hoped in the future to give some account of the microscopic features of those parts which prove to be in a suitable state for histological examination.

Specimens of the brain of the fin-whale (*Balaenoptera physalis*), common porpoise (*Phocaena phocaena*) and of the bottle-nose dolphin (*Tursiops truncatus*) were available for comparison.

GENERAL FORM AND DIMENSIONS

As may be seen from the figures (Text-fig. 1, Pl. 1, figs. 1, 2), the general form and proportions of the various parts of the brain conform to the typical cetacean pattern. One notes the marked brachyencephaly, the exuberant folding of the cerebral cortex, the almost vertical disposition of the Sylvian fissure with its surrounding series of concentric sulci, and the large size of the cerebellum.

The two halves of the brain are reasonably symmetrical, except for the cerebellum, the right half of which appears to be somewhat smaller than the left. However, each half weighs approximately the same, and this applies as well to the two halves of the entire brain. It is probable that in brains of this size minor degrees of asymmetry such as have been noted by previous authors, e.g. Guldberg (1885) may depend upon the position in which they happened to be placed during fixation, although this does not appear to be entirely the case where the odontocete brain is concerned (cf. Kojima, 1951).

Certain dimensions of the brain are given below. Unfortunately, nothing is known of the body dimensions of the individual (a female) from which the specimen was removed.

Weight

Entire brain without dura	4030 g.
Cerebellum	740 g.
Cerebellar percentage of total	18 %

Linear

Antero-posterior diameter of cerebral hemisphere	18.0 cm.
Dorso-ventral diameter of cerebral hemisphere	15.0 cm.
Transverse diameter of cerebral hemisphere	12.0 cm.
Transverse diameter of cerebellum	15.0 cm.
Cranio-caudal diameter of pons	3.5 cm.
Transverse diameter of pons (between fifth nerves)	3.5 cm.

VENTRAL ASPECT OF THE BRAIN AND ORIGIN
OF THE CRANIAL NERVES

This is illustrated in Text-fig. 1, and since the arrangement is practically identical with that found in other cetaceans, little comment is necessary.

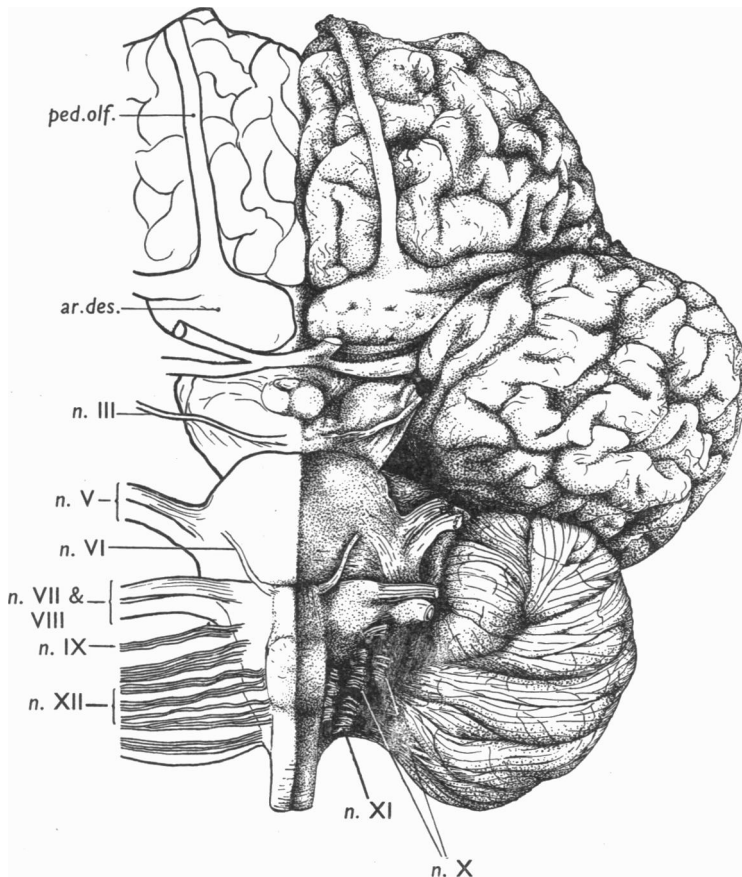
The olfactory peduncle measured 18 cm. in length, was 4 mm. wide and 1.5 mm. thick. As such it is somewhat wider and thicker than the human olfactory peduncle (3×1 mm.) and on section was seen to be composed of numerous fine nerve fibres. The olfactory bulb was not present, so presumably the peduncle was longer than the figure quoted by an unknown amount. Macroscopic medial and lateral olfactory tracts were not observed, but the diagonal band was very evident, a characteristic feature of the cetacean brain (Breathnach, 1953). Distinct mamillary bodies could not be identified.

The fifth is the largest of the cranial nerves and springs from the pons in a manner similar to that in the fin-whale (Jansen, 1953). The proximal portion is filamentous, the more distal and larger part forming a solid trunk. A prominent obliquely directed bundle of pontine fibres descends between the origin of this nerve and that of the seventh, and may correspond to the oblique bundle of the pons of human anatomy.

The eighth nerve comes next in size to the fifth. It is interesting to note that there appears to be a distinct difference between the two groups of Cetacea so far as the relative macroscopic sizes of these two nerves are concerned. In the Mysticeti (present account; Wilson, 1933; Jansen, 1953) the fifth is the larger, whereas in the Odontoceti (Langworthy, 1932; Ries & Langworthy, 1937) the reverse is the case, and the acoustic centres in the mid-brain are relatively larger.

The ninth nerve is slender and arises by a series of obliquely placed rootlets caudal and medial to the origin of the eighth (Text-fig. 1). The tenth and eleventh nerves (Text-fig. 1; Pl. 2, figs. 3, 4) arise in a manner similar to that figured by Jansen (1953) in the fin-whale. The tenth is comprised of two series of rootlets, medial and lateral which may as suggested by Jansen correspond to the motor and sensory roots respectively of the vagus. The bulbar portion of the accessory nerve

is in direct linear continuity caudally with the medial rootlets of the vagus, and the spinal portion (Pl. 2, fig. 3) springs from the lateral aspect of the spinal medulla opposite the first two cervical segments. The twelfth nerve arises by a series of ten to twelve rootlets lateral to the olivary eminence, which in cetacea is formed by the prominent medial (accessory) olive. The pyramids are small and cannot be seen below the level of the upper border of the olive over the surface of which the fibres are spread.



Text-fig. 1. A drawing of the ventral aspect of the brain to show the origins of the cranial nerves. $\times 0.5$.

MEDIAN SAGITTAL SECTION OF BRAIN STEM

This is figured in Pl. 1, fig. 2. The corpus callosum is of moderate size and has an orientation typical for cetaceans. There is no rostrum and the cavum septi is open as in the porpoise (Breathnach, 1953). The margin of the fornix towards the septum pellucidum is difficult to define, and in this situation it forms a much less compact bundle than, for instance, in the porpoise.

The depth of the third ventricle greatly exceeds the antero-posterior diameter,

a characteristic cetacean feature which can be associated with the shape of the brain as a whole. An ill-defined small anterior commissure could be observed half-way up the lamina terminalis, but it does not show particularly well in the figure. Well-marked preoptic and infundibular recesses are present in the floor of the ventricle, which is particularly thin in the mid-line of the tuberal region. The inter-thalamic connexus is extensive and accentuates the well-marked hypothalamic sulcus which lies ventral to it. The pineal could not be identified and may have been removed with the membranes. In this regard it is of interest to note that Fuse (1936) found the pineal to be rudimentary in the series of cetaceans examined by him, whereas Gersch (1938) had no difficulty in identifying it in the humpback.

The aqueduct is voluminous, another typical cetacean feature (Ries & Langworthy, 1937). A considerable portion of the lateral wall is formed by the tectum, and a small recess extends laterally between the posterior aspect of the inferior colliculus and the superior medullary velum. (This is accentuated somewhat in the photograph by a slight detachment of the velum in this situation.) The velum is extensive and can be followed posteriorly as far as the apex of the median dorsal recess of the IVth ventricle. The cerebellum is described later (p. 348).

CEREBRAL HEMISPHERES

A markedly convoluted surface with the fissures on the lateral aspect arranged in an arcuate manner around the Sylvian fissure is characteristic of the cetacean cerebral hemisphere. The temporal lobe is markedly developed. These features can be seen in Text-fig. 1, and Pl. 1, figs. 1 and 2.

Previous authors (Guldberg, 1885; Rawitz, 1910; Kojima, 1951, etc.) have been much concerned about the comparative homology of the cerebral fissures of cetaceans, but their labours have produced little result beyond varying degrees of disagreement over the naming of particular fissures, largely because of a lack of criteria suitable for their identification. In the case of certain fissures, e.g. the rhinal, which separate cortical areas of widely differing structure, histological examination may help in identification (Breathnach, 1953), and in the case of others such as the sulcus cinguli, topographical relations may help. As regards the majority of fissures on the supero-lateral surface, however, one can merely speculate, and as this is likely to be a particularly barren exercise, no attempt is made in the present account to enter into this matter.

A well-marked Sylvian fissure is present (Pl. 1, fig. 1) at the bottom of which an extensive area of operculated cortex is found covering the lateral aspect of the corpus striatum. Following the practice of other authors (e.g. Guldberg, 1885) this may be called the 'insula'. Topographically it certainly corresponds with the insula of human and other primate brains, but whether the correspondence extends to cytoarchitectonic features such as those used by Rose (1928) to define 'insular cortex' it is not yet possible to say. In the humpback whale the Sylvian fissure is almost completely closed; in *Balaenoptera sibbaldi* Beauregard (1883) found it widely open, and Wilson (1933) described the insula as being almost entirely exposed in *Balaenoptera sulphurea*. Comparison between the humpback and fin-whale brains in our possession shows that the fissure is more widely open in the latter. From a

study of the literature it would appear that in spite of considerable variation there is a general tendency for the fissure to be more open in the Mysticeti than in the Odontoceti.

MESENCEPHALON

The cerebral peduncle is short and wide (Text-fig. 1), and a number of the surface fibres take an oblique course. A well-marked, narrow transverse peduncular tract (Pl. 2, fig. 4) can be traced along the lateral aspect from the neighbourhood of the upper edge of the superior colliculus to a point somewhat proximal and lateral to the origin of the third nerve. This tract has also been noted by Wilson (1933) in *Balaenoptera* and by Kojima (1951) in *Physeter*.

The tectum is large and forms not only the roof but a considerable portion of the side wall of the large aqueduct. There is a marked difference in shape between the two colliculi, and because of this, it is very difficult to give an accurate estimate of their relative sizes. Viewed from the dorsal (Pl. 2, fig. 3) and medial (Pl. 1, fig. 2) aspects, the superior one appears to present the greater surface area, while on lateral view the inferior is by far the larger (Pl. 2, fig. 4). The overall impression gained by macroscopic examination is that the inferior colliculus has the larger volume, although a definite answer can only be reached on microscopic examination. Guldberg (1885), in his account of the brain of a foetal humpback, described the inferior colliculus as being the smaller. According to Wilson (1933) the inferior colliculus is larger in *Balaenoptera sulfurea* (although it is difficult to obtain an adequate impression from his figures), and Langworthy (1935) found the same to be the case in *B. physalis*. In the Odontoceti (e.g. *Tursiops* and *Physeter*), however, as pointed out by Langworthy, the reverse relationship holds, the inferior being the larger. It is possible that this apparent difference between the two groups may be correlated with the fact that the eighth nerve appears to be larger in the Odontoceti. However, estimates of size based upon surface appearances may be misleading, and one must be cautious of drawing functional conclusions from evidence of this character.

A broad mass of fibres connects the colliculi of opposite sides across the mid-line, and it is not easy to distinguish a distinct posterior commissure. The brachium of the inferior colliculus is easily recognized, and the lateral lemniscus forms a stout band as it emerges from the pons to pass backwards deep to the inferior colliculus (Pl. 2, fig. 4). The slender fourth nerve springs from the angle formed between the lateral lemniscus and the superior cerebellar peduncle a considerable distance from the mid-line. The medial geniculate body is prominent (Pl. 2, fig. 4), but the lateral geniculate produces no recognizable surface elevation.

MEDULLA AND PONS

The salient features of the ventral aspect have been described already and are illustrated in Text-fig. 1.

The cavity of the fourth ventricle is voluminous (Pl. 1, fig. 2), but remarkably little detail can be distinguished in the floor. There is no sign of striae medullares, and neither hypoglossal nor facial eminences can be defined (Pl. 2, fig. 3). The longitudinal bundle of fibres labelled 'medial longitudinal bundle' by Langworthy

(1932) in the porpoise, and also noted by Jansen (1953) in the fin whale, can be seen faintly. This absence of surface features which is in contrast to the findings of the above authors in the animals named, does not appear to be due to poor preservation of the material. A corresponding lack of detail was noted by Wilson (1933) in *Balaenoptera*.

CEREBELLUM

The cetacean cerebellum has attracted considerable attention in the past, partly on account of its large size. Amongst those who have previously attempted an analysis of the folial pattern may be mentioned Guldberg (1885), Bolk (1906) and Ogawa (1935). Unfortunately, most of these accounts are unsatisfactory largely because of differences in the terminologies used, but also because little or no embryological material was available with which to check the validity of the interpretation of the condition in the adult.

By far the most satisfactory account of the cetacean cerebellum is contained in the recent work of Jansen (1953, 1954) which is based upon a unique collection of graded foetal as well as adult material from the fin-whale. His identification of the various subdivisions differed so much from that of previous workers that it was considered of value to determine how closely his scheme can be applied to the cerebellum of the humpback whale.

Jansen adopts the usual subdivision into anterior and posterior lobes (comprising the corpus cerebelli) and a flocculo-nodular lobe. A similar subdivision can be used for the humpback whale; the fissura prima, separating anterior and posterior lobes can be readily identified in median section (Text-fig. 2) and can be followed into the hemispheres of the cerebellum (Text-fig. 3). The postero-lateral fissure can also be seen in median section (Text-fig. 2) where it separates the small nodule of the flocculo-nodular lobe from the uvula of the posterior lobe; its lateral extension will be described later.

The anterior lobe (Text-figs. 2, 3 and 5)

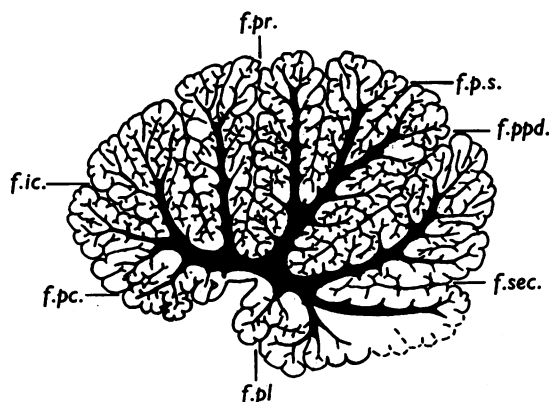
In median section (Text-fig. 2) the vermis of the anterior lobe in the humpback whale is practically identical with that of the fin-whale (see Jansen, 1954, fig. 20), and comprises about one-third of the area of the arbor vitae. Jansen's praeculminate and intraculminate fissures can easily be identified.

The hemispherical parts of the anterior lobe (Text-fig. 3) are small, as is generally the case in Cetacea (Jansen, 1953); that they appear somewhat larger in the humpback whale than in Jansen's illustration of the fin-whale is mainly due to a slight difference in the orientation of the specimens from which the figures were drawn.

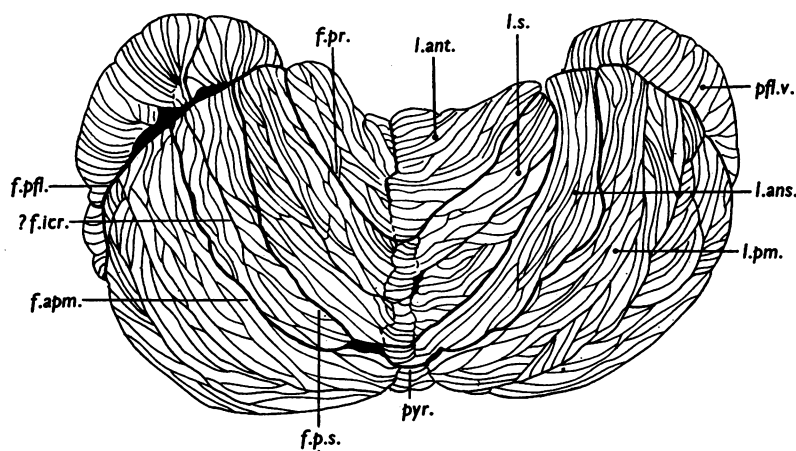
The posterior lobe (Text-figs. 2-5)

In median section (Text-fig. 2) the similarity to the fin-whale is not quite so marked as in the anterior lobe. There seems little doubt about the identification of the postero-lateral fissure, the fissura secunda and the praepyramidal fissure, defining the uvula and the pyramid of the vermis. These indeed resemble the corresponding parts in the fin-whale very closely. Cranial to the praepyramidal fissure, however, Jansen (1954) identifies two fissures in the fin-whale, the intercrural and the postero-superior fissures respectively. The postero-superior fissure, traced

laterally (Text-fig. 3), forms the posterior boundary of the lobulus simplex and on that account can be identified in the humpback whale and has been marked on the median section (Text-fig. 2). It is not so deep as in the fin-whale. The intercrural fissure, following Jansen, should be between the postero-superior and the praepyriformal fissures and can be traced (in the fin-whale) laterally into



Text-fig. 2. Mid-sagittal section of cerebellum. Drawn from a photograph. $\times 0.8$.



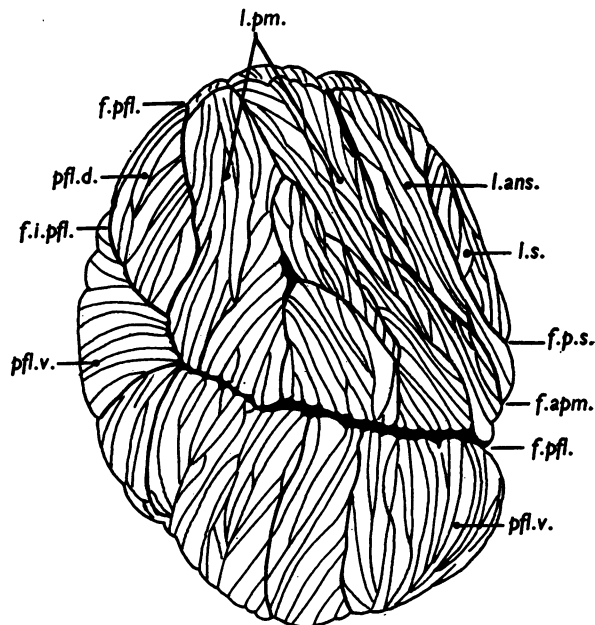
Text-fig. 3. The fissures and lobules on the dorsal aspect of the cerebellum. Drawn from a photograph. $\times 0.5$.

the ansiform lobule where it separates Crus I from Crus II. Apart from the very shallow indentation seen in median section in the humpback whale (Text-fig. 2, unlabelled) no such fissure is present in the vermis in this animal.

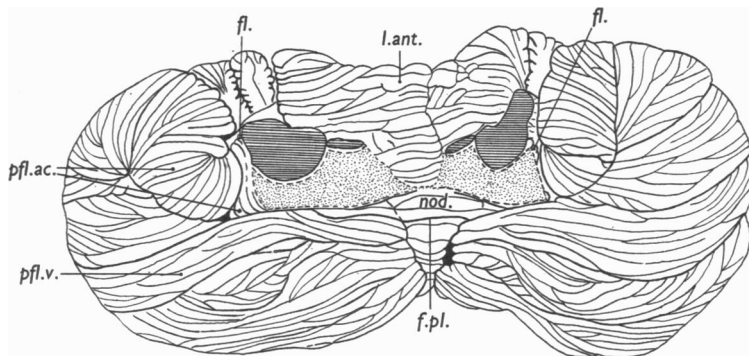
The hemispherical parts of the posterior lobe are the lobulus simplex, the ansiform lobule, the paramedian lobule and the paraflocculus.

The lobulus simplex forms the most cranial subdivision and lies between the fissura prima and the postero-superior fissure. It corresponds fairly closely in relative size and extent with Jansen's (1954) concept of this lobule in the fin-whale.

The ansiform lobule lies immediately behind the postero-superior fissure and is bounded caudally by the anso-paramedian fissure (Text-fig. 3). In the adult fin-whale Jansen (1954) described the anso-paramedian fissure as 'being apparently



Text-fig. 4. The fissures and lobules on the lateral aspect of the cerebellum.
Drawn from a photograph. $\times 0.8$.



Text-fig. 5. Ventral view of cerebellum. Drawn from a photograph. $\times 0.5$.

continuous with the prepyramidal fissure on the surface, but stated that closer examination revealed several cortical lamellae which passed across the bottom of the praepyramidal fissure to connect the paramedian with the median part of the ansiform lobule (or tuber vermis). In effect, therefore, the anso-paramedian fissure swings on to the oral bank of the prepyramidal fissure. Since an exactly similar

arrangement is found in the humpback whale, there seems no doubt about the identification of the anso-paramedian fissure as marked in Text-fig. 3, and it should be noted that the ansiform lobule is considerably smaller than in the fin-whale. Moreover, as already pointed out, there is difficulty in defining an intercrural fissure in the humpback whale. It has been indicated tentatively on the left side of Text-fig. 3, but it does not reach the mid-line and nothing corresponding can be found on the right. While no doubt the cranial and caudal parts of the ansiform lobule represent Crus I and Crus II, as defined by Jansen in the fin-whale, it is clear that the subdivision between them is poorly indicated.

The paramedian lobule was defined by Jansen (1954) as 'bordered by the anso-paramedian and parafloccular fissures and medially continuous with the posterior tuber and the pyramis'. The portion of the cerebellar hemisphere in this position in the humpback whale is very similar in shape and extent with Jansen's paramedian lobule (Text-fig. 3). It forms nearly the whole of the lateral aspect of the cerebellum dorsal to the paraflocculus (Text-fig. 4) and is the second largest lobule of the cerebellum.

The paraflocculus forms the remainder of the posterior lobe between the fissura parafloccularis and the postero-lateral fissure. According to Jansen (1953) it is relatively enormous in Cetacea and he divides it into three parts, dorsalis, ventralis and accessorius.

The fissura parafloccularis can be readily identified in any cetacean cerebellum as the deep fissure which appears to divide the hemisphere into two main parts (Text-figs. 3, 4). Jansen (1953) defines the dorsal paraflocculus as an oval lobule lying between this fissure and the fissura intraparafloccularis. A lobule which is practically identical in appearance with the dorsal paraflocculus of Jansen's account is present in the humpback whale (Text-fig. 4). Medially it is continuous with the most rostral folia of the uvula.

The great size of the ventral paraflocculus, as well as the position of the accessory paraflocculus, may be seen from Text-figs. 4 and 5. These portions of the hemisphere have an extent and appearance closely similar to those of the same name figured by Jansen (1954) in the fin-whale. It should be noted that in this publication Jansen included in the accessory paraflocculus the part labelled *p. fl. v. x.* in his 1953 account in addition to the group of folia lying deep to it (his original accessory paraflocculus).

Flocculo-nodular lobe (Text-figs. 2, 5)

The position of the postero-lateral fissure on the median section can be seen from Text-fig. 2. On the ventral aspect the vermian portion of this fissure is clearly defined (Text-fig. 5) and when traced laterally, it appears to extend in such a manner as to necessitate including a part which obviously corresponds with the deeper part of the accessory paraflocculus of Jansen's (1953) account, within the flocculo-nodular lobe as part of the flocculus. Closer examination, supplemented by a study of the fin-whale material available (where the condition of the flocculo-nodular lobe is identical with that figured by Jansen) indicated that this was an erroneous interpretation due to the fact that the intermediate portion of the postero-lateral fissure is extremely shallow in places. This is a condition which is apparently quite common

in adult animals, cf. Larsell (1953), and may explain previous misinterpretations of the extent of the flocculus in cetacean brains.

The flocculus in the humpback consists of five to six poorly developed folia which partly cover over the roof of the lateral recess (Text-fig. 5) and are connected medially with the nodule by means of an attenuated peduncle composed of two or three very narrow folia. This condition is identical with that found by Jansen (1953) in the fin-whale.

From the above description it will be seen that Jansen's scheme of cerebellar subdivision fits the folial pattern as seen in the humpback whale very closely. The only large difference encountered was the small size of the ansiform lobule and the absence of a well-developed fissura intercruralis. This lobule seems to be particularly liable to variation in size and arrangement in different animals, and at present no great significance can be attached to its small size in the humpback whale.

DISCUSSION

It is clear that the brain of the humpback whale (*Megaptera novaeangliae*) does not differ markedly from those of other Mysticeti, and there are few matters which call for discussion so far as the gross morphology is concerned.

A feature of the cetacean brain to which attention has frequently been drawn is the reduction or absence of the olfactory apparatus, and it is of interest to note that the olfactory peduncle in the humpback is of considerable size and contains a considerable number of olfactory tract fibres. The condition of the olfactory mucosa, the primary receptor surface, is not known, but the central neurological part of the olfactory apparatus has certainly been preserved to a much greater extent than in the Odontoceti and would appear capable of functioning. Whether olfaction plays any important part in the life and behaviour of the animal is, however, extremely doubtful, since the blow-hole is closed except during the brief periods when the animal is on the surface. It seems more likely that the olfactory apparatus in the Mysticeti is comparable to the muscles of the human auricle, which, while preserving all the neurological connexions necessary for active function, play no significant part in human behaviour. The fact that the olfactory bulbs and peduncles have been completely lost in the Odontoceti supports this hypothesis.

It is commonly thought that olfactory connexions are of considerable importance in determining the morphology of the forebrain as a whole, and this is probably true in the early stages of the evolution of vertebrates. Once the basic pattern of the forebrain is established, however, the fate of the olfactory apparatus seems to be of very limited significance. This conclusion was reached by Armstrong, Gamble & Goldby (1953) as a result of their examination of the brain of *Anolis*, a microsmatic lizard, and is supported by the conditions in cetaceans. The differences between the brains of the Mysticeti and the Odontoceti can be attributed far more plausibly to the differences in the morphology of the skull, than to the presence of olfactory tracts in the one and their absence in the other. It is indeed probable that the loss of the olfactory bulbs and tracts in the Odontoceti is itself related to mechanical factors in the development of the skull, as suggested by Howell (1930). These must be very different from those obtaining in the Mysticeti, although the final result in the 'telescoping' of the cranial cavity is somewhat similar in both groups (Miller, 1923).

Langworthy (1981) has pointed out that the acoustic division of the eighth nerve is probably the paramount sensory cranial nerve in living cetaceans, and it is tempting to relate the greater development of the acoustic nerve and centres in the odontocete as compared with the mysticete brain with the lesser development of the olfactory connexions in the former. There is, however, no reason whatever for postulating a reciprocal relationship between these two nerves of special sense; either might rise to dominance, or become suppressed, quite independently of the other.

In the cerebellum it can be seen that the subdivisions recognized by Jansen (1953, 1954) in the fin-whale can all be readily identified in the humpback whale, and that the relative proportions of the different parts are almost exactly similar. While, in the absence of foetal material, the present study can give no information about the sequence of appearance of the fissures, the similarity in the adult stages makes it very probable that Jansen's findings in the fin-whale would be equally applicable to the humpback whale.

SUMMARY

1. The surface appearances of the brain of the humpback whale are described. Apart from differences in size the arrangement does not differ appreciably from that of other mysticete brains which have been described.

2. Jansen's scheme of cerebellar subdivision fits closely to the pattern found in the humpback whale.

Thanks are due to Mr R. M. Brachi, and Messrs Hector Whaling Ltd., London, for collecting the specimen; to Prof. F. Goldby for advice and criticism; and to the Photographic Department, St Mary's Hospital Medical School, for the photographs which appear in Pls. 1 and 2. Text-fig. 1 was drawn by Miss Jill Payne.

ABBREVIATIONS FOR ALL FIGURES

<i>ar.des.</i>	area désert	<i>hyp.</i>	hypophysis
<i>aq.cer.</i>	aqueductus cerebri	<i>l.ans.</i>	lobulus ansiformis
<i>br.pont.</i>	brachium pontis	<i>l.ant.</i>	lobus anterior
<i>c.cal.</i>	corpus callosum	<i>l.pm.</i>	lobulus paramedianus
<i>ch.</i>	chiasma opticum	<i>l.s.</i>	lobulus simplex
<i>col.inf.</i>	colliculus inferior	<i>lem.lat.</i>	lemniscus lateralis
<i>col.sup.</i>	colliculus superior	<i>n. II-XII</i>	cranial nerves
<i>cor.gen.med.</i>	corpus geniculatus medialis	<i>nod.</i>	nodulus
<i>f.apm.</i>	fissura anso-paramedianus	<i>ped.olf.</i>	pedunculus olfactorius
<i>f.i.pfl.</i>	fissura intra-parafloccularis	<i>pfl.ac.</i>	paraflocculus accessorius
<i>f.ic.</i>	fissura intraculminata	<i>pfl.d.</i>	paraflocculus dorsalis
<i>f.icr.</i>	fissura interculturalis	<i>pfl.v.</i>	paraflocculus ventralis
<i>f.p.s.</i>	fissura postero-superior	<i>pyr.</i>	pyramis cerebelli
<i>f.pc.</i>	fissura praeculminata	<i>str.t.</i>	stria terminalis
<i>f.pfl.</i>	fissura parafloccularis	<i>tr.opt.</i>	tractus opticus
<i>f.pl.</i>	fissura postero-lateralis	<i>tr.ped.</i>	tractus peduncularis transversus
<i>f.ppd.</i>	fissura praepyramidalis	<i>thal.</i>	thalamus
<i>f.pr.</i>	fissura prima	<i>v. IV</i>	ventriculus quartus
<i>f.sec.</i>	fissura secunda	<i>v.lat.inf.</i>	ventriculus lateralis (cornu inferior)
<i>f.syl.</i>	fissura sylvia	<i>v.med.ant.</i>	velum medullare anterior
<i>fl.</i>	flocculus		
<i>for.</i>	fornix		

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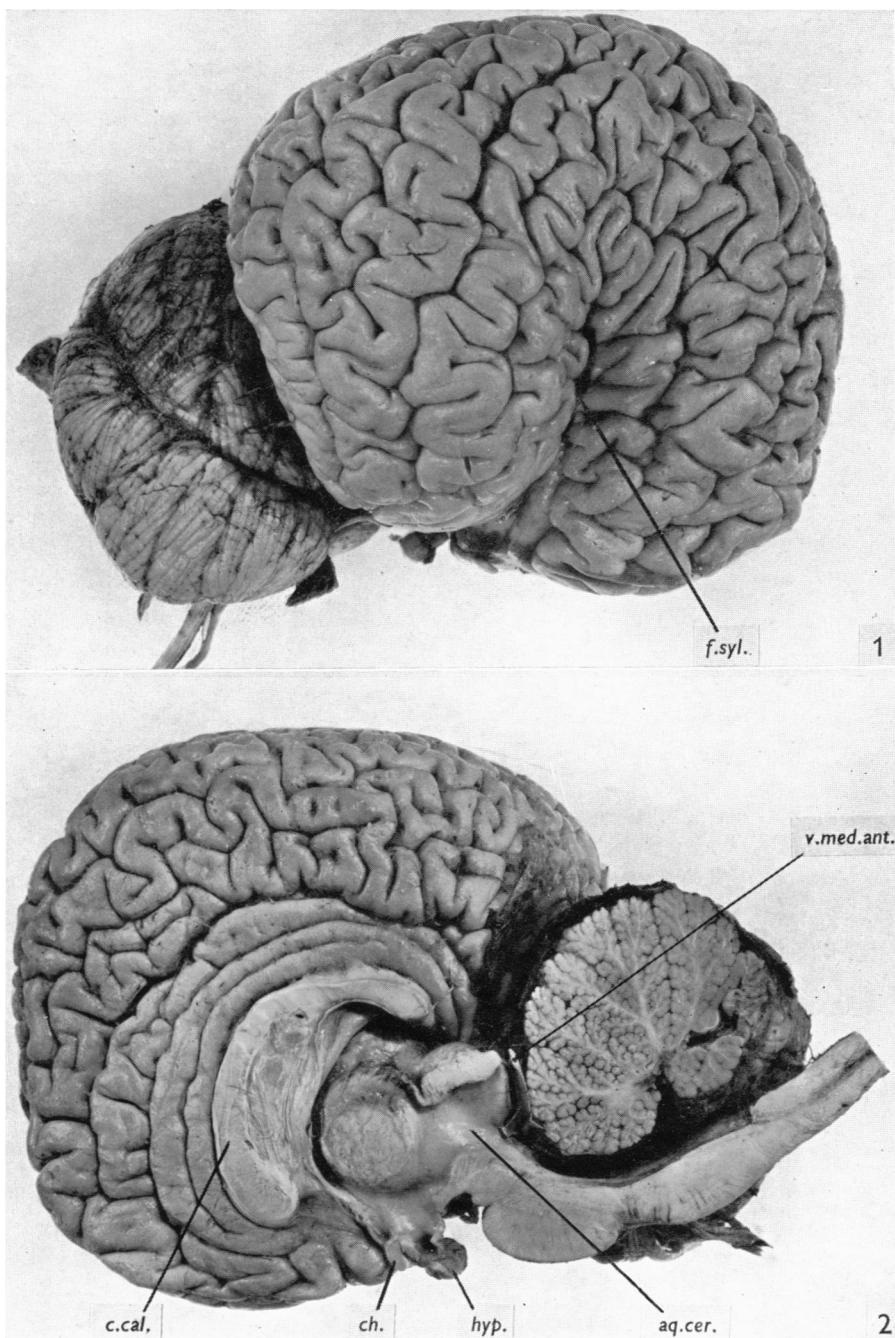
EXPLANATION OF PLATES

PLATE 1

Figs. 1 and 2. Lateral and median sagittal aspects of the brain of *Megaptera novaeangliae*. × 0.5.

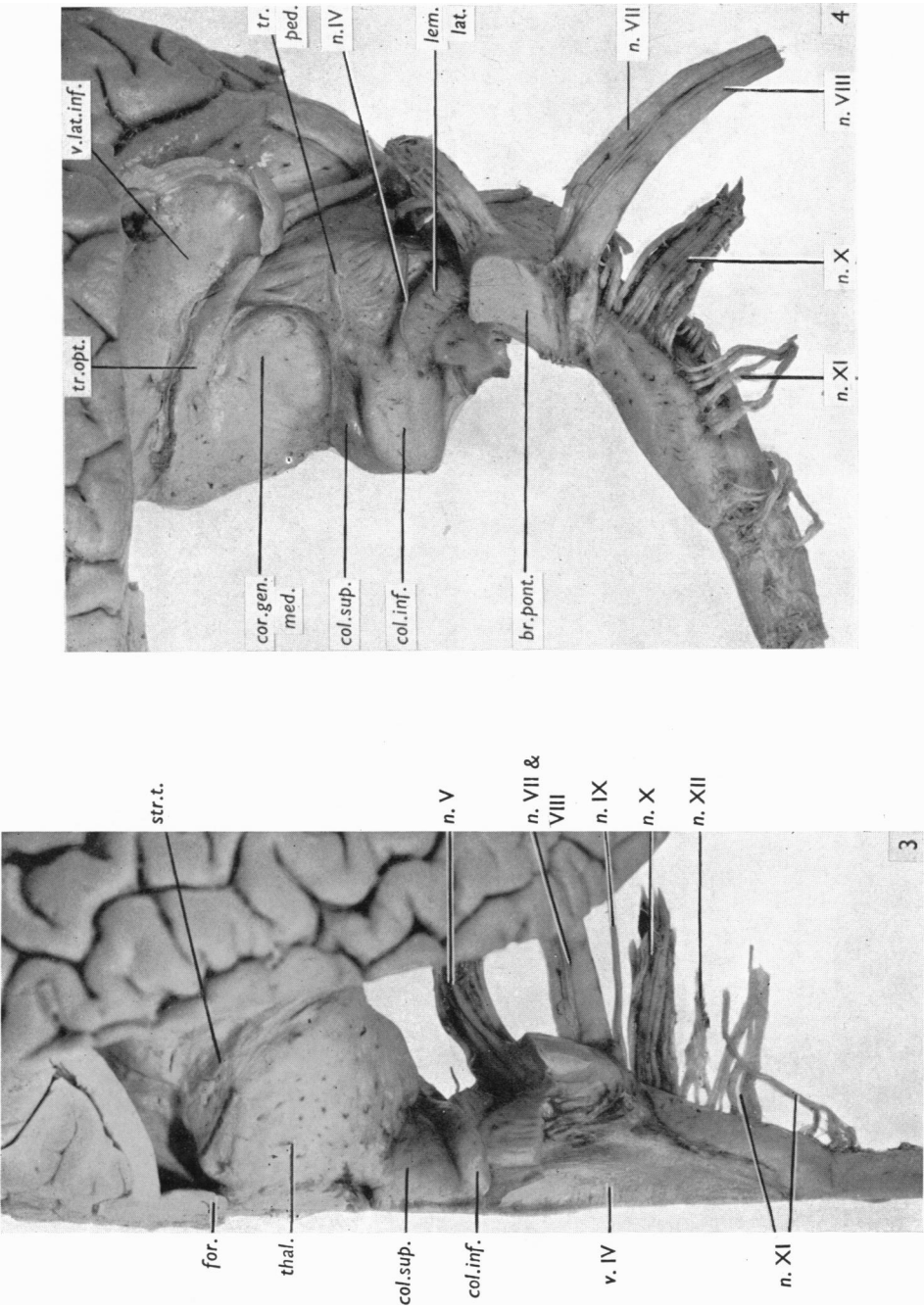
PLATE 2

Figs. 3 and 4. Dorsal and lateral aspects of the brain stem of *Megaptera novaeangliae*. × 0.6.



BREATHNACH—THE BRAIN OF THE HUMPBACK WHALE

(Facing p. 354)



BREATHNACH—THE BRAIN OF THE HUMPBACK WHALE